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Delayed reproduction suggests a phenological response to fire in *Pithecopus ayeaye* (Anura: Hylidae: Phyllomedusinae)

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Amphibians exhibit remarkable diversity in reproductive modes, with more than 40 modes currently recognised across the clade (Haddad & Prado 2005, Malagoli et al. 2021). This variety is unparalleled among vertebrates and reflects the multiple evolutionary trajectories enabling amphibians to adjust their reproduction to environmental pressures (Haddad & Prado 2005, Crump 2015). Terrestrial reproduction, for instance, has evolved multiple times and is often considered an adaptation conferring significant advantages, including the avoidance of aquatic predators, reduced larval competition, reproductive independence from temporary ponds, decreased exposure to aquatic parasites and diseases and diminished potential for scramble competition (Lutz 1948, Magnusson & Hero 1991, Prado et al. 2002, Todd 2007, Zamudio et al. 2016). As a trade-off, terrestrial reproduction entails risks not faced in aquatic environments, particularly the vulnerability of eggs to desiccation and predation by other vertebrates and invertebrates and their sensitivity to disturbances that affect microhabitats used for oviposition (Crump 2015, Batista et al. 2023). This balance between the costs and benefits has contributed to the evolution of diverse reproductive strategies but also increases sensitivity to environmental disturbance (Haddad & Prado 2005, Silva et al. 2012).

One phytogeographical domain where these selective pressures are particularly acute is the Brazilian Cerrado, a Neotropical savanna covering approximately two million square kilometres in central South America (Eiten 1972, Machado et al. 2023). Widely recognised as a biodiversity hotspot (Myers et al. 2000), fire is a natural and recurrent disturbance that has shaped Cerrado landscapes for millennia, and its vegetation is well adapted to frequent burning and edaphic constraints (Coutinho 1990, Neves & Conceição 2010, Le Stradic et al. 2018). This domain hosts an extraordinary assemblage of plants possessing morphological and physiological traits that facilitate persistence in fire-dominated environments, including underground buds, resprouting capacity, fire-stimulated germination and anatomical structures that buffer against heat damage (Pausas et al. 2018, Pilon et al. 2020, Fidelis & Zirondi 2021). The 'campo rupestre', one of its most distinctive physiognomies, is a fire-prone ecosystem characterized by herbaceous-shrubby vegetation on rock outcrops and shallow, nutrient-poor soils (Silveira et al. 2016). Hosting a high heterogeneity of habitats and fire-resilient, adapted species, fire has been shown to be an important driver shaping vegetation in this ecosystem (Neves & Conceição 2010, Pausas et al. 2018, Le Stradic et al. 2018). In contrast, animal responses remain less understood and are particularly poorly documented for amphibians (González et al. 2022), with no specific fire-related adaptations reported in 'campo rupestre' so far (Oswald et al. 2025). However, animal responses in this system likely rely largely on behavioural strategies to mitigate fire impacts, such as seeking refuge, fleeing disturbed areas, or shifting activity patterns in space and time (Pausas & Parr 2018, Schäfer et al. 2022).

Amphibians are presumed to be especially vulnerable to fire due to their dependence on moist microhabitats, permeable skin, relatively limited dispersal ability and reliance on specific oviposition sites (Wells 2007). Fire may act directly by destroying nests, clutches, or plants used for oviposition, or indirectly by altering microclimatic conditions and vegetation structure in ways that reduce reproductive opportunities and food availability (Rocha et al. 2008, van Mantgen et al. 2015, González et al. 2022, Batista et al. 2023, Ribeiro et al. 2025). While adult frogs might survive through behavioural plasticity, the early reproductive stages, eggs and larvae, are often less resilient (Batista et al. 2023). In species that rely on vegetation structures for oviposition, fire may have particularly strong reproductive consequences by removing the physical substrates required for egg deposition. An open question is whether amphibians in fire-prone ecosystems can adjust reproductive timing to compensate for temporary losses of habitat structure, particularly in tropical savannas where fire occurs with predictable frequency. Despite the intuitive importance of this question, evidence remains scant (Ribeiro et al. 2020, Anjos et al. 2021, Ribeiro et al. 2025). Moreover, direct observations of fire events coinciding with amphibian reproductive activity are inherently rare, as such disturbances are unpredictable and often occur outside the temporal window of biological monitoring. Consequently, opportunistic observations may provide some of the few empirical insights into how fire affects amphibian reproduction in natural systems. *Pithecopus ayeaye* (Hylidae: Phyllomedusinae; Fig. 1) provides an important model for investigating this question because it relies on vegetation to construct leaf nests for egg deposition (Oliveira 2017, Borges et al. 2018), and may therefore be vulnerable to fire effects on its terrestrial clutches. This Cerrado endemic species is associated with rocky streams and shrubby vegetation in the 'campo rupestre' of southeastern Brazil (Del Prette et al. 2024). Its reproductive mode, classified as mode 25 (*sensu* Haddad & Prado 2005), involves oviposition on the adaxial surface of leaves projecting above the water, using temporary streams for tadpole development. During egg deposition, females fold the leaf around the clutch, potentially reducing desiccation risk and concealing the eggs from predators (Crump 2015, Oliveira 2017). The tadpoles subsequently hatch directly into the stream, bypassing terrestrial or lentic aquatic stages. The reproductive season of *P. ayeaye* typically spans from October to February, coinciding with the onset of the rainy season in the Cerrado. This strategy is highly dependent on the presence of overhanging shrubs and broad leaves, which are critical for oviposition (Oliveira 2017, Borges et al. 2018). Consequently, any disturbance reducing the availability of such vegetation could have cascading effects on reproduction. Although the general ecology of the species has been described, its responses to habitat disturbance remain poorly understood. Here we report an opportunistic observation of a fire event occurring during the reproductive season of *P. ayeaye* and examine its immediate consequences for the availability of oviposition substrates and breeding activity in a 'campo rupestre' stream.

On 22 September 2024, a fire swept across Serra do Lenheiro, a 'campo rupestre' area in São João del-Rei, Minas Gerais state, southeastern Brazil (21°06'58.94" S, 44°16'36.36" W, WGS84, 1003 m.a.s.l), burning intensely through shrubby riparian vegetation along small rocky streams (Fig. 2). This event created a unique opportunity to assess the potential impact of fire on the reproduction of *P. ayeaye* by comparing data collected before and after the disturbance. We initiated systematic monitoring of a local population in October 2022 and continued through March 2023, encompassing one full reproductive season prior to the fire. Following the fire, monitoring was repeated from October 2024 to March 2025, capturing a second reproductive season under post-fire conditions.

Monitoring consisted of nocturnal monthly surveys along a fixed 250 m transect in a rocky stream. Pre-fire surveys comprised eleven sampling events conducted between October 2022 and March 2023, each consisting of two observers sampling for four hours (total effort = 88 observer-hours). Post-fire surveys comprised seven sampling events conducted between October 2024 and March 2025, following the same protocol of two observers sampling for four hours per event (total effort = 56 observer-hours). Surveys were conducted at approximately monthly intervals in both periods. Observers varied among sampling events; however, at least one observer in each survey had prior experience with the study system and with the sampling protocol. All observers were trained using the same search method, and survey procedures remained identical before and after the fire. This design ensured comparable detectability of egg clutches across sampling periods despite minor variation in observer identity.

During each survey, all shrubs overhanging the water were carefully inspected for egg clutches. For each nest encountered, we recorded the date and clutch condition, distinguishing among nests with hatched clutches, viable nests containing embryos with normal development, and

Figure 1. Adult male individual of *Pithecopus ayeaye* from the Serra do Lenheiro population, Minas Gerais, Brazil. Photo by G. C. S.

unviable clutches that were desiccated, fungal-infected, or predated. We tallied the monthly number of nests to reconstruct reproductive phenology and compared the total number of nests, the proportion of inviable clutches, and the timing of reproductive activity between the pre-fire and post-fire seasons. To assess the potential influence of precipitation, we compared clutch data with monthly rainfall records corresponding to all survey periods. Rainfall data were obtained from the São João del-Rei meteorological station (A514), located approximately 3 km from the sampling site, and provided by the Instituto Nacional de Meteorologia (INMET). These data were used to qualitatively evaluate whether differences in precipitation between seasons could explain shifts in reproductive phenology independently of fire effects (Table 1).

During the first reproductive season (2022–2023), we recorded a total of 81 nests. Oviposition began in October, shortly after the onset of rains, and peaked between November and December, declining gradually through January. This pattern is consistent with previous accounts of the species (Oliveira 2017, Borges et al. 2018). During the second season (2024–2025), however, only 48 nests were observed and reproductive activity extended into February. Notably, the reproductive peak of the species differed between the two periods, occurring in November, before the fire, and in January after the fire (Fig. 3). The proportion of inviable clutches was similar between the two periods (approximately 8.64% before the fire and 10.48% after), suggesting that egg survival per se was not strongly affected. The key difference appeared to be the delayed onset of reproduction, which coincided with the slow regrowth of shrubby vegetation along the stream margins (Fidelis & Zirondi 2021); such vegetation remained scarce until early January (Fig. 2).

Table 1. Precipitation and number of nests.

Period	Year	Month	Monthly precipitation (mm)	Number of nests
Pre-fire	2022	October	134.6	10
Pre-fire	2022	November	201.6	29
Pre-fire	2022	December	393.2	24
Pre-fire	2023	January	515.8	18
Pre-fire	2023	February	257.8	0
Pre-fire	2023	March	113.6	0
Post-fire	2024	October	193.8	5
Post-fire	2024	November	328.6	6
Post-fire	2024	December	234.2	9
Post-fire	2025	January	291	27
Post-fire	2025	February	48.2	1
Post-fire	2025	March	119.4	0

Precipitation did not directly track reproductive activity, despite rainfall typically acting as a primary cue for amphibian reproduction, generally stimulated by precipitation (Oliveira 2017). In the pre-fire season, rainfall increased from November to January while the number of nests declined over the same period (Fig. 3). In contrast, during the post-fire season, reproductive activity remained low in November despite the onset of rains and peaked only in January, when precipitation was already decreasing (Fig. 3). Moreover, although rainfall was relatively low in January of the post-fire season, nest numbers were substantially higher than those recorded earlier in the same season, further suggesting that precipitation alone does not explain the observed phenological shift. Nevertheless, cumulative

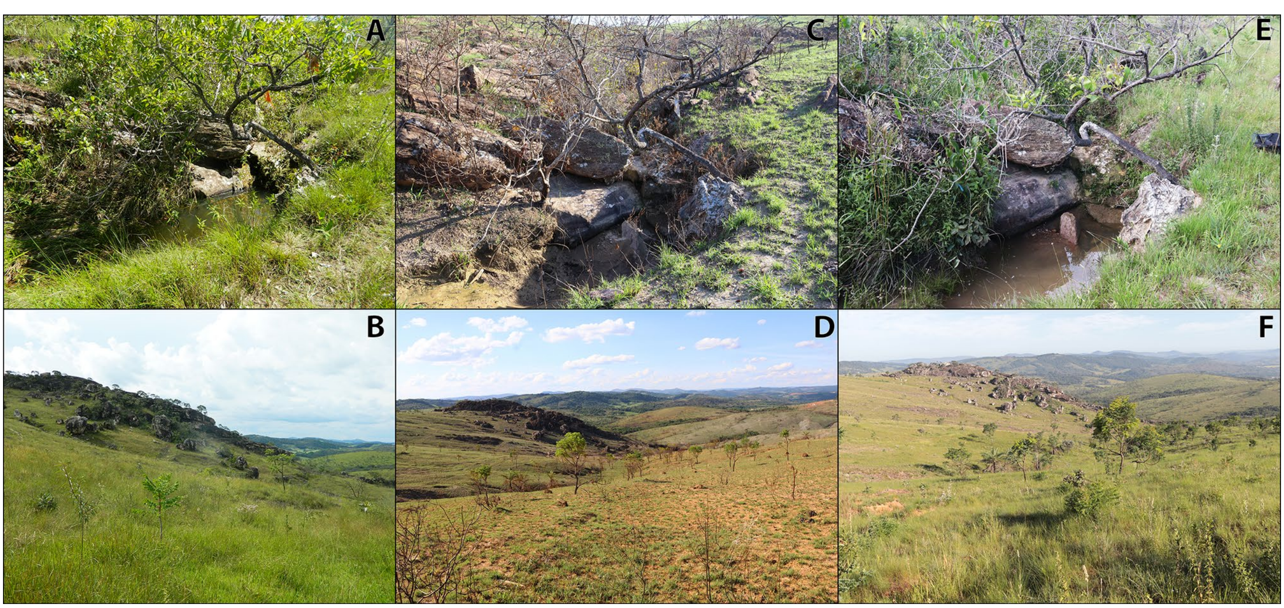

Figure 2. Effects of the fire in the study area: (A, B) in October 2023 before the fire; (C, D) in October 2024, shortly after the fire; (E, F) in February 2025.

rainfall was lower overall in the post-fire season, particularly from December onwards, which may have reduced water accumulation in the stream. Thus, while the delayed reproductive peak coincided with post-fire vegetation loss, we cannot rule out a synergistic effect in which reduced water availability combined with fire-driven habitat alteration contributed to the change in reproductive timing.

A limitation of this study is the difference in sampling effort between monitoring periods. However, egg clutches of *P. ayeaye* are highly conspicuous and remain detectable even after hatching. Eggs hatch approximately 12–15 days after oviposition, but the folded leaves typically persist as closed or semi-open funnels, often retaining dried gelatinous material inside the nest, as well as the gelatinous capsules deposited at the leaf tips. These features allow nests to be recognized well beyond the embryonic period (unpubl. data). Therefore, the pronounced difference in clutch numbers between periods, together with the coincidence of the reproductive peak with post-fire vegetation recovery, suggests that variation in sampling effort likely had little influence on the observed pattern.

These observations suggest that the fire might not have reduced reproductive success through direct increases in clutch mortality, but rather through the temporary loss of suitable oviposition sites. The reproductive phenology of anurans is directly linked to abiotic factors involved in reproduction, such as precipitation, temperature, and the availability of breeding sites (Gottsberger & Gruber 2004, Fava et al. 2023, Lenzi et al. 2023). In the absence of an adequate supply of broad leaves above water, females likely postponed reproduction until vegetation recovery reached a threshold permitting oviposition. The consequence was a compression of the reproductive period into a shorter timeframe, with potential implications for recruitment and population dynamics. While a delay of two months may not necessarily compromise reproductive output in a single season, recurrent fires or shorter rainy seasons could exacerbate the mismatch between reproductive timing and environmental conditions.

Our results highlight a potential form of behavioural plasticity in *P. ayeaye*: the adjustment of reproductive phenology in response to vegetation dynamics after fire. This also underscores that even species with highly specialised reproductive modes may exhibit some degree of temporal flexibility, possibly allowing them to buffer short-term habitat fluctuations. At the same time, the relatively small number of nests observed post-fire raises concerns about population resilience under scenarios of increasing fire frequency or intensity. Responses to fire depend on both the intrinsic traits of species and the characteristics of the fire itself, such as intensity, size, rate of spread, season of occurrence, and fire history, which can have significant effects on species abundance and distribution (González et al. 2022). If fires occur at intervals shorter than the time required for shrubs to recover, or if climatic shifts alter rainfall regimes, the ability of *P. ayeaye* to maintain viable populations could be compromised.

The broader implications extend to amphibian ecology in fire-prone ecosystems generally. Studies on amphibians and the effects of fire are still scarce, with most being concentrated in temperate regions and mainly at the community level (González et al. 2022). In Neotropical savan-

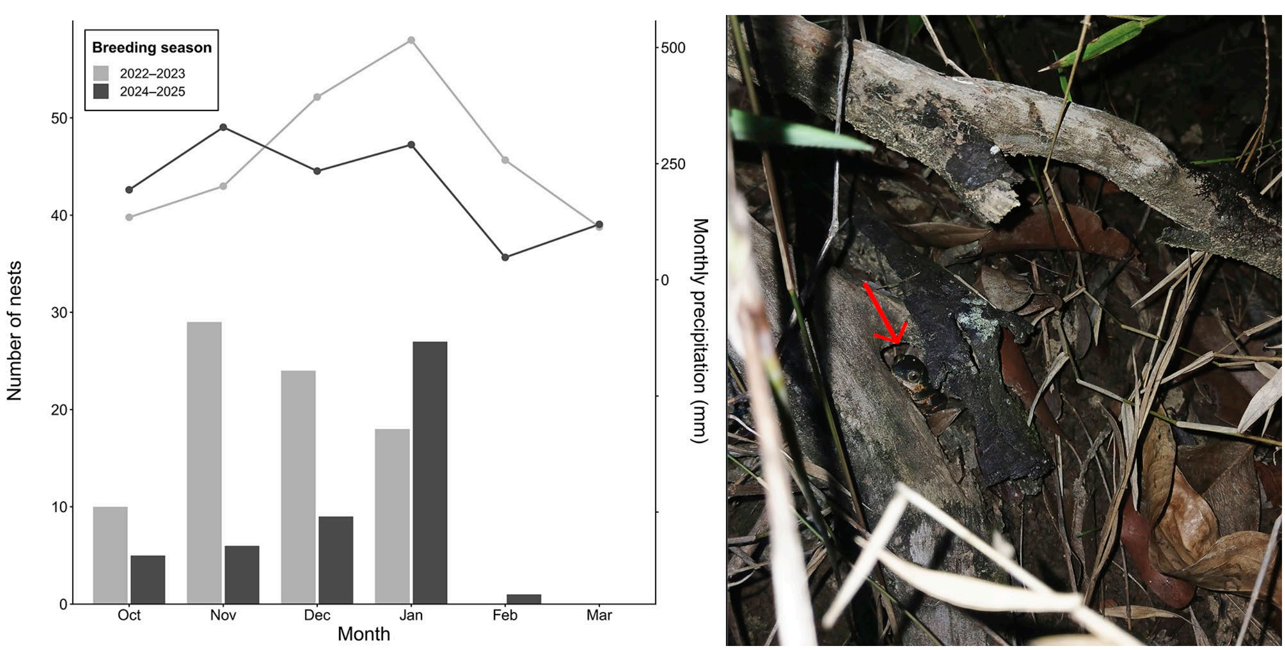

Figure 3. Left, number of egg clutches of *Pithecopus ayeaye* between the months of October and February for the pre-fire (2022–2023) and post-fire (2024–2025) periods and average monthly precipitation for the same period obtained from Meteorological National Institute (INMET, https://portal.inmet.gov.br/); right, individual hiding in a hole of a burnt tree trunk after the fire (arrow).

nas, indirect effects mediated through vegetation dynamics may be of great importance. Amphibians that depend on plants for reproduction, particularly those with terrestrial or arboreal modes, are likely to be especially vulnerable (Papp & Papp 2000, Jolly et al. 2022, Batista et al. 2023, Moreira et al. 2023). The case of *P. ayeaye* demonstrates that reproductive timing can shift to accommodate vegetation recovery, but also that this shift may come at the cost of reduced reproductive output and compressed breeding periods, affecting population recruitment.

Our study, although based on a single population and two consecutive breeding seasons, suggests that reproduction in *P. ayeaye* is constrained by the availability of broad leaves overhanging water, indicating a close link between vegetation structure and phenological plasticity. The delay in oviposition observed after the fire likely reflects a behavioural adjustment to the temporary scarcity of suitable substrates, rather than a direct effect on clutch survival. This interpretation is consistent with the similar proportion of inviable clutches between periods and with the progressive recovery of shrubby vegetation along stream margins. The ability to postpone reproduction may vary among individuals or populations, potentially influencing resilience to disturbance, but the demographic consequences of delayed breeding remain uncertain, particularly under variable rainfall regimes. A previous study on another population of *P. ayeaye* in 'campo rupestre' reported no population fluctuations following fire (Drummond et al. 2018), suggesting that responses may depend on local vegetation recovery, fire characteristics, or climatic conditions. Future studies incorporating experimental manipulation of vegetation cover, long-term monitoring across multiple fire events, and demographic analyses will be essential to evaluate the generality of these mechanisms and their consequences for recruitment.

Understanding amphibian responses to fire is increasingly urgent under global change. In the Cerrado, natural fire regimes are being altered by human activities, with fires becoming more frequent, extensive, and sometimes more intense than historical patterns (Pivello et al. 2021), while climate change may disrupt rainfall predictability and the synchrony between vegetation recovery and amphibian reproductive cycles (Forti et al. 2022). Although fire is an important component of savanna biodiversity (Durigan 2020), its effects on amphibians remain poorly understood, particularly in the Brazilian anurofauna (Anjos et al. 2021). Our results provide evidence that fire can alter reproductive phenology in a species with specialised oviposition requirements, reducing the number of spawning events and compressing the breeding period. The delay observed in *P. ayeaye* suggests that phenological flexibility may provide short-term buffering against habitat loss, but this mechanism may be insufficient under recurrent disturbances or slower vegetation recovery. These findings highlight the importance of considering indirect effects of fire on reproductive substrates and demonstrate that monitoring reproductive phenology can be a valuable tool for assessing amphibian responses and guiding conservation and fire management strategies in Neotropical savanna ecosystems.

Our results provide evidence that fire can shift reproductive phenology in a Neotropical amphibian with a specialised reproductive mode. To our knowledge, this represents one of the first field-based demonstrations of a delayed breeding response associated with post-fire vegetation loss in anurans, a mechanism that has been largely hypothesised but rarely documented (Anjos et al. 2021, González et al. 2022). The delayed reproduction observed in *P. ayeaye* is most consistently explained by a vegetation-mediated effect, in which the fire reduced the availability of broad leaves overhanging streams, temporarily limiting suitable oviposition sites and postponing breeding activity until vegetation recovery. This mechanism highlights that fire may influence amphibian populations not only through direct mortality or habitat alteration, but also through indirect effects on reproductive substrates. Species that depend on plants for oviposition, particularly those with terrestrial or arboreal reproductive modes, may therefore be especially sensitive to changes in post-fire vegetation structure. Under scenarios of increasing fire frequency and intensity in the Cerrado (Pivello et al. 2021), such delays may compress breeding seasons, reduce reproductive output, and ultimately affect recruitment. These findings emphasise the importance of considering vegetation-mediated pathways when assessing fire impacts on amphibians and suggest that monitoring reproductive phenology can provide an effective tool for detecting early demographic responses in fire-prone savanna ecosystems.

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